

ORIENTED LIGHT REACTIONS OF THE ARROW WORM *SAGITTA* *CRASSA* TOKIOKA

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ABSTRACT

The arrow worm *Sagitta crassa* shows positive phototaxis in a horizontal light beam by repeatedly swimming briefly upward with the body axis inclined toward the illuminated side, and then by passively sinking. Phototactic behavior is less evident in vertical beams. When a horizontal light beam is reduced after a period of illumination, the arrow worms have a fast goal seeking response, steering themselves toward the reduced light source in less than 0.3 s and swimming straight to this target at rates greater than 14 cm/s. When two light targets are presented immediately after a reduction in light intensity, the arrow worms choose the brighter one, indicating that the response may be a type of telotaxis. The two kinds of phototactic swimming may be explained by slow taxis by changes in orientation, and target-aiming behavior by two sequential processes: an arousal increase followed by an activity release.

INTRODUCTION

Chaetognaths, commonly called arrow worms from their elegant appearance and swimming behavior, are a small, phylogenetically isolated group of marine planktonic predators. Next to copepods, they are the commonest component of the zooplankton. Consequently, they are important in pelagic ecosystems. Apart from field studies on diurnal vertical migration patterns (Michael, 1911; Russell, 1927, 1931; Murakami, 1959; Pearre, 1973; Nagasawa and Marumo, 1975; Kotori, 1976; Hirota, 1979; Goto, 1980), little is known about physical factors that control their pattern of swimming behavior. Esterly (1919) and Pearre (1973), working with *Sagitta bipunctata* and *S. elegans* respectively, show that both these species are strongly photopositive in a horizontal light beam, negatively geotactic in a vertical tube in darkness, and positively geotactic in a bright light. We present below our detailed analyses of light oriented movements (phototaxis) in *Sagitta crassa*, including a new type of a target-aiming (telotactic) quick swimming behavior.

MATERIALS AND METHODS

Arrow worms, *Sagitta crassa*, were collected at night by slowly towing horizontally XX 13 gauge net (mesh size 95 μm square). To avoid unduly damaging the worms, a small collecting bottle, 13 cm in diameter and height, with a leak pipe at the center, was held at the cod end of the net. Mature worms at Stage III of Pierce's classification (1951) captured in this manner were maintained in a seawater-filled trough (23 cm in diameter and 10 cm in height) at 17°C under a cycle of 12 h light:12 h darkness. Worms could be kept healthy for at least 3 weeks by keeping less than 10 in each trough, feeding them with freshly hatched *Artemia salina* nauplii every 3 days, and changing the seawater at each feeding.

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Abbreviations: $-\Delta I$, light intensity reduction; L₁, L₂, target lights; CL, conditioning light.

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Tungsten filament lamps (100 V, 150 W) were used as light sources. The light beam which passed through infrared absorbing filters (Toshiba IRA 25 S) and neutral density filters (Toshiba), was made approximately parallel by a lens system. Details of experimental procedures are described below.

RESULTS

Slow tactic behavior

A shallow transparent trough ($20 \times 4 \times 4$ cm) was used. At the start of each experiment, a worm adapted to darkness for longer than 10 min was placed in a 5 cm compartment behind a partition that was 15 cm from the wall of the trough and that faced a horizontally directed light source. Positively phototactic swimming behaviors were examined by removing the partition and simultaneously opening the shutter of the light source, and counting numbers of worms that reached the illuminated side within 10 min. Most worms responded positively to moderate intensities of light (Fig. 1, curve A) and remained at the illuminated region of the trough, moving back and forth to a small extent. This effect was less pronounced with the brightest light.

Phototactic worms did not swim directly toward the light source. Instead, while responding positively (Fig. 1, curve B), they shifted their position in a series of upward swimming and downward maneuvers, rather like the "hop and sink" behavior described for other plankton (Fig. 2). Close examination of the path followed shows that the body axis of the upward swimming worms tended to be inclined toward the light source.

These inclination angles were measured by photographing with strobe flashes every 15 s for 2 min while worms were kept in darkness (control) or were exposed to a horizontal light beam of various intensities. Results (Fig. 3) show that in a horizontal light beam of 500 lux (B), about three times as many arrow worms incline toward the light than away from it ($60.3 \pm 7.1\%$ vs. $18.4 \pm 3.5\%$). Such preferred inclination will result in progressive movement toward the light, since arrow worms do not swim backward. The frequencies between inclinations toward and away from light appeared to differ in darkness (35.6% vs. 43.1%) as well as

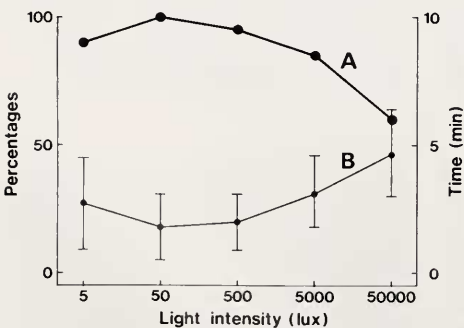


FIGURE 1. (Left) Phototaxis in a horizontal light beam. A: Percentages of positively phototactic worms ($n = 20$). B: Time required for the positively responded worms to reach the illuminated end. Vertical bars: Standard deviation.

FIGURE 2. (Right) Photograph taken by 30 s continuous exposure, showing a typical phototactic trail of an arrow worm in a thin tank (8×1.5 cm, 6 cm deep). Light (5000 lux) entering from the right. Scale: 1 cm.

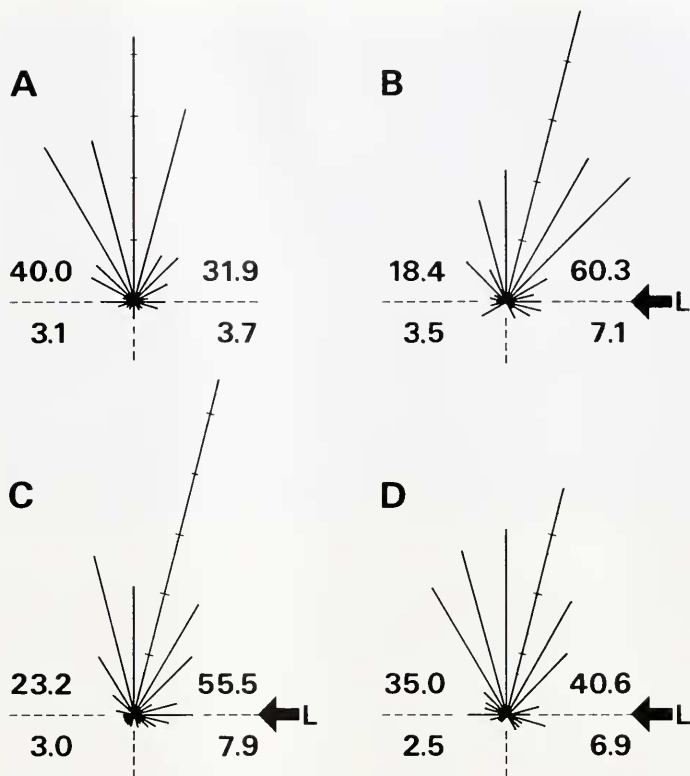


FIGURE 3. Incline pattern of the body axis of worms measured at 15-degree intervals in darkness (A: Dark control, $n = 163$) and in a horizontal light beam (B: 500 lux, $n = 141$. C: 5000 lux, $n = 164$. D: 50,000 lux, $n = 160$). Lengths of each radiating line show the percentages of worms inclined in that direction (calibrations on the longest line show 5% intervals). Since upright (90°) and upside down (270°) orientations are irrelevant to the light oriented responses, the number of worms which took such orientations were summed separately. Numbers in each quadrant are total percentages in the respective direction.

in the bright light (47.5% vs. 37.5%). But the difference was insignificant ($0.3 < P < 0.5$ and $0.2 < P < 0.3$, respectively), indicating random movements.

If movement to the end of the experimental vessel illuminated by a horizontal beam is achieved by repeated inclined vertical movements, a vertical beam will not be as effective in attracting *Sagitta* as it has been reported to be in directly phototactic planktonic crustaceans. This was found to be true. Thus, few worms reached the illuminated water surface or bottom of a deep container (4×4 cm, 40 cm high) in downward- or upward-directed beams (Fig. 4A, curves a and b, respectively). Those animals presumably attracted to these points did not stay but soon swam away, though some animals remained in the middle and lower sections with upward directed beams (white bars in Fig. 4C). On the other hand, the fact that most of the worms were found in the upper region of the container after a dark period (initial distribution pattern; black bars in Fig. 4B, C) indicates that the worms are basically negatively geotactic. The increase in numbers in the middle and lower sections with brighter downward directed beams (white bars in Fig. 4B) indicates that light changed the sign of geotaxis.

Quick target-aiming behavior

While maintaining worms with an overhead light, we noticed that when the aquarium was shifted, a majority of the worms swam briskly straight toward the lamp side. Similar rapid responses were seen when the intensity of a horizontal light beam was suddenly reduced. Trails photographed by a continuous exposure (e.g., Fig. 5) showed that this swimming pattern was different from that of the ordinary hop and sink phototactic behavior (Fig. 2). The response proceeded in two steps: First, the worms oriented themselves toward the reduced light source. Second, they swam straight toward it.

Cine camera recordings (36 frames per s) showed that the orientation was completed within 0.3 s and that the swimming speed was more than 14 cm per s. The rapid swimming is not achieved by an initial single stroke of the tail. Figure 5 shows brighter profiles (representing slow speed movements) at intervals along the more or less straight, faint (high speed) trails, indicating repeated successive bursts of rapid swimming. Other photographs show that swimming speed increased during the target-aiming response.

Effects of light-intensity reduction. We studied the effects of different amounts of light intensity reduction ($-\Delta I$) in evoking rapid swimming. In this and all the following experiments, experimental animals were selected on the basis of their ability to respond to 90% reduction of a horizontal light intensity of about 1000 lux, after 3–5 min illumination with this light. Such worms were assumed to be healthy. (Damage or deterioration might have occurred during collection and maintenance.) Usually about 30% of the worms collected met this behavioral criterion.

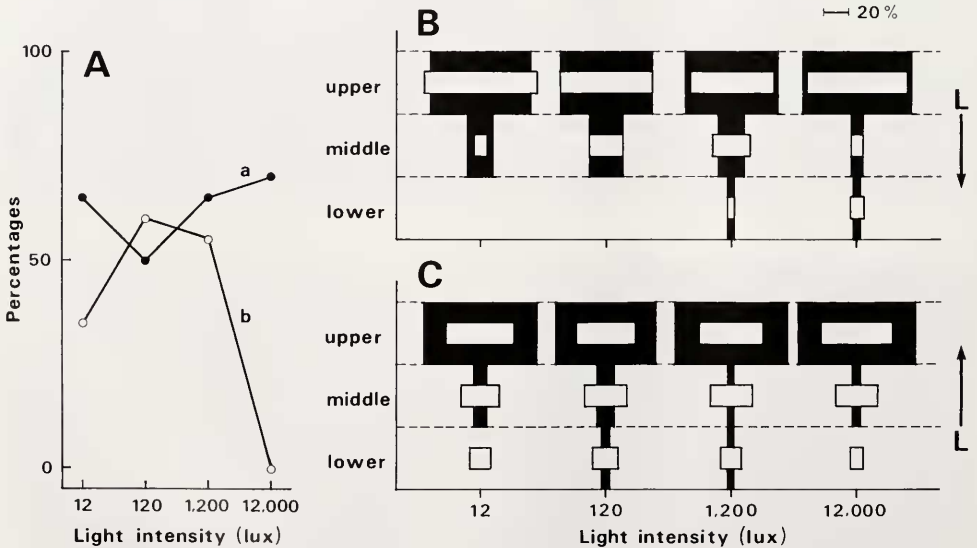


FIGURE 4. Phototaxis in vertical light beams. A: Percentages of worms ($n = 20$) which reached the water surface at least once with a downward directed beam, curve a, or the bottom of the tank with an upward directed beam, curve b. B and C: Vertical distribution patterns at the beginning (initial, black bars) and end (final, white bars) of a 10 min illumination period with either downward (B) or upward (C) directed beams after dark adaptation for 10 min. "Upper," "lower," and "middle" on the left designate, respectively, the upper one tenth (4 cm), lower one tenth (4 cm), and middle section (32 cm) between the two of a deep container.



FIGURE 5. Photograph taken by a 3 s continuous exposure, showing an arrow worm's pattern of target-aiming swimming. Light (50,000 lux) directed from the right was reduced by 90%. Note that the worm, which had been inclined toward the left, changed its body axis to the right almost instantaneously: No trail linking the left-oriented posture to the right appears on the photograph, indicating a very quick change sequence. Scale: 1 cm.

In each experiment, a light-adapted worm was placed in a trough 20 cm long, 4 cm wide, and 4 cm deep, which was illuminated from both ends, one end at 800 lux and the other varying from 160–2400 lux. After 5–10 min, the fixed-intensity light was turned off and whether the worm oriented and swam toward the remaining light was recorded (Fig. 6). The larger $-\Delta I$, the more worms swam toward the light. The mechanisms involved in the response's two steps (steer and swim) differed in sensitivity, so that a majority only steered themselves upon small $-\Delta I$'s, whereas all the animals went on to the second step (swim) in response to the largest $-\Delta I$.

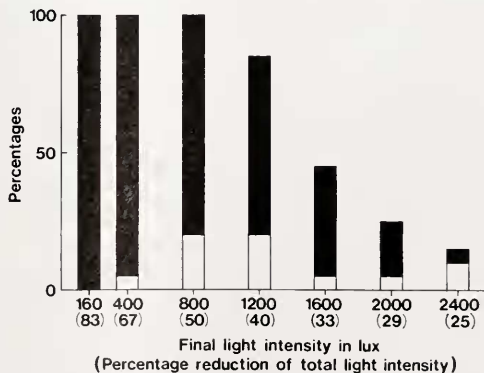


FIGURE 6. Target-aiming response following intensity reduction by extinguishing a light of 800 lux from one end, showing percentages of worms ($n = 20$) that steered (white bars) or steered and swam (black bars) toward the remaining light at the opposite end of the trough (abscissa). The reduction in intensity is indicated in brackets along the abscissa.

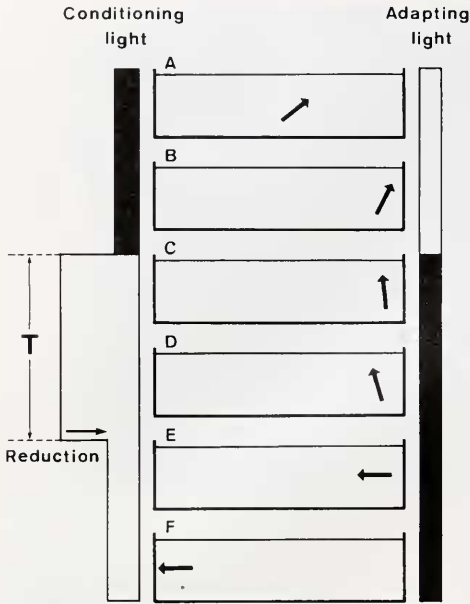
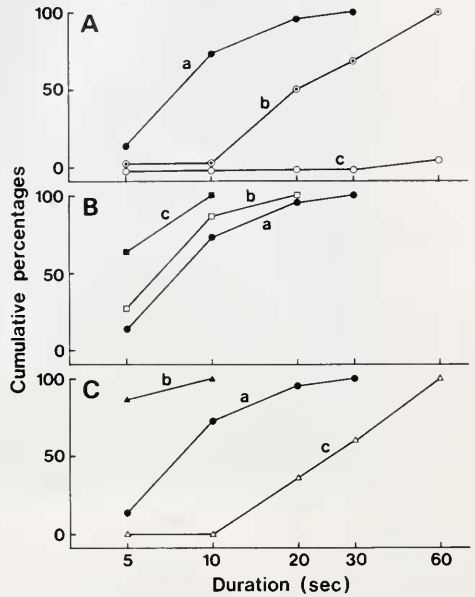


FIGURE 7. (Left) Schematic representation of the sequence of photic manipulations for testing rapid target-aiming behaviors. Arrows indicate arrow worms. T: Duration of illumination with the conditioning light. A: Illumination with an adapting light for 5–10 min. B: The worm reaches the illuminated end. C: Turning on of a conditioning light and off of the adapting light. D: The worm is illuminated by the conditioning light for a period of T. E: Orientation of the worm toward the conditioning light when it is reduced (arrow to the right). F: Quick swimming toward the reduced light source.

FIGURE 8. (Right) Effects of photic conditions on the critical period, the shortest duration of illumination with the conditioning light necessary to induce the target-aiming swimming (abscissa). The ordinate shows cumulative percentages of worms ($n = 22$) that responded with a critical period shorter than that on abscissa. Curves *a* are the same in all three figures (A, B, C). Photic conditions that varied are the degree of reduction in A (*a*, 90%; *b*, 70%; *c*, 50%), the intensity of the conditioning light in B (*a*, 600 lux; *b*, 180 lux; *c*, 60 lux) and the intensity of the adapting light in C (*a*, 12 lux; *b*, 120 lux; *c*, 0 lux).



Effects on response threshold of adapting and conditioning lights. To elucidate physical factors necessary to induce these responses, we manipulated light conditions as follows (Fig. 7): A dark adapted worm was put in the trough and an adapting light on one end was turned on for 5–10 min (A). Within this period, the worm reached the illuminated end by its positive phototaxis (B). Another conditioning light on the opposite side was then turned on, while the adapting light was simultaneously turned off (C). After a certain period of illumination (T) the intensity of the conditioning light was reduced suddenly by interposing neutral density filters (E).

Thus, photic conditions that might affect responses are the intensities of the adapting and conditioning lights and $-\Delta I$'s. The effectiveness of each photic condition may be expressed by the shortest illumination time (to be called a critical period) necessary to induce the responses. In the experiments, critical periods were determined by stepwise increases (5, 10, 20, 30, 60 s, or longer) until the worm responded to $-\Delta I$. When no response was induced with a given period of illumination, each worm was dark adapted for 5 min before starting the next step with 5–10 min illumination by the adapting light.

Experiments were performed by varying one of the three photic factors while keeping the other two constant (Fig. 8). When $-\Delta I$ was varied (Fig. 8A), only one of 22 worms responded to 50% reduction within a critical period as long as 60 s (curve c). A 70% reduction (curve b) made the critical period shorter than 60 s in all the worms tested, and 20 s was long enough to induce responses in half the worms tested. A 90% reduction made the critical period mostly shorter than 10 s. Thus, the larger the $-\Delta I$, the shorter is the required duration of the conditioning illumination. Conversely, longer conditioning exposures lower the threshold for $-\Delta I$. Indeed, when the worms were exposed to 1600 lux for more than 30 min, a 25% reduction induced rapid swimming behavior.

Under varying intensities of the conditioning light with 90% $-\Delta I$ (Fig. 8B), the critical periods were about the same under 180 lux and 600 lux (curves a and b) but became shorter under 60 lux (curve c). Figure 8C shows the results of varying the adapting light intensities with a 90% reduction of a 600 lux conditioning light. With no adapting light, the critical period became significantly longer (curve c). When, however, the intensities of the adapting light were equal to (60 lux; not shown in the figure) or higher than (120 lux) the reduced level of the conditioning light (60 lux), a shorter illumination (less than 10 s) with the conditioning light induced the response in all the worms tested (curve b). Thus, the adapting light that was used to lead worms to one side of the experimental vessel also increased the readiness of the worms to respond to an intensity reduction.

However, $-\Delta I$ was not the only stimulus that induced such rapid target-aiming responses. A single mechanical shock to the container—knocking, shifting, etc.—was sometimes effective. As shown in Figure 9, more animals orient toward the light source in response to single mechanical shocks as illumination is prolonged. This implies that during light adaptation, worms become ready (arousal) to orient themselves toward the light when stimulated by a releasing signal, which may be a light intensity reduction, a mechanical shock, or some other stimulus. Following orientation, responding worms would next swim directly to the target. Indeed, totally shaded worms swam around briskly but in random directions, as they had no obvious goal. The initial changes of the body axis toward the light, which occurred as a first step in Figure 5, must indicate that the worm can locate the target visually.

Effects of two stimuli. To determine what worms would do given two targets, the following experiments were performed, using three light sources (Fig. 10A, B): Worms put in the trough were illuminated by the conditioning light (1500 lux) for 10 min. Target lights (I_1 , I_2) were then turned on and the conditioning light (CL) simultaneously extinguished. The intensity of I_2 was varied in a range between 18 and 600 lux while keeping I_1 at 120 lux, and the number of times the worms chose each target was determined. Most worms that responded to $-\Delta I$ aimed at target I_2 when I_2 was brighter than 150 lux (Fig. 10C). Since all the worms tested moved toward one of the two targets, a plot of percentages of worms that moved toward the target I_1 would be a mirror image of the curve in Figure 10C.

Some of the worms chose a dimmer target when I_2 was in the range 60–150 lux (25% in 60 lux and 15% in 150 lux). However, as the 50% level of the curve passes near the 120 lux line, where the intensities of the two targets were equal, the worms apparently made a 50–50 or random choice in this range. Therefore, worms aroused to be ready to respond will steer toward the brighter of two targets when released by an intensity reduction.

Effects of vertical light sources. As was done with horizontal lights, responses

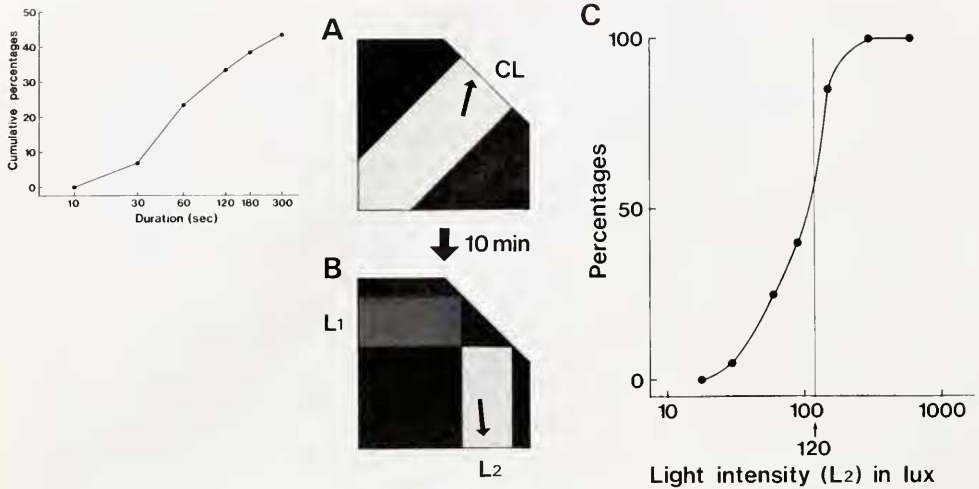


FIGURE 9. (Left) Effects of a mechanical shock on the orientation reaction of the body axis toward the light source (400 lux). Ordinate: Cumulative percentages of worms ($n = 60$) which responded with a critical period shorter than that shown on the abscissa. The mechanical shock was given by a solenoid which was triggered by a condenser discharge and which shifted the trough by 0.8 mm in 15 msec at an initial rate of 6 cm/s.

FIGURE 10. (Right) Choice of two targets. A and B show a trough and lighting conditions. CL: Conditioning light (1500 lux). L₁ (120 lux) and L₂ (varied: 18–600 lux) served as targets. Lighter stipplings indicate brighter light. Black arrow indicates an arrow worm. In C, percentages of worms ($n = 20$) which moved toward L₂ are plotted on the ordinate. Abscissa: Intensity of L₂ relative to L₁, whose (fixed) level is shown by an arrow.

in vertical light beams directed from above or below were examined by determining the critical period necessary to induce responses to various $-\Delta I$'s (Fig. 11). The procedure differed slightly, however. Single worms in each experiment were placed in the deep container under a dim red light (longer than 600 nm in wavelength). An adapting light (Fig. 7) was not used: Test illuminations began after 5 min dark adaptation.

As shown in Figure 11C, when the downward directed light beams of 3000 lux were reduced to 300 lux, critical periods were extremely long (curve d). Large $-\Delta I$'s, down to 30 lux, shortened the critical period markedly (curve c); and with even deeper shadings, to 3 and 0 lux (curves b and a, respectively), 30 s illumination induced responses in most worms. However, those upward movements may have been due to target-aiming or to negative geotaxis in darkness following elevated kinetic activity induced by light-intensity reduction.

Reduction of light directed from below was more effective in inducing rapid downward swimming. When the light was reduced to 300 or 30 lux, all the worms responded with critical periods shorter than 2 min (curves c and d in Fig. 11B). If, however, the beam intensity was reduced to 0–3 lux, a considerable number of worms swam upward (curves a' and b' in A), possibly due to geo-negativity in darkness.

DISCUSSION

Diurnal vertical migrations of arrow worms in the sea, rising at dusk and sinking at dawn, have been noted frequently (Michael, 1911; Russell, 1927, 1931; Mu-

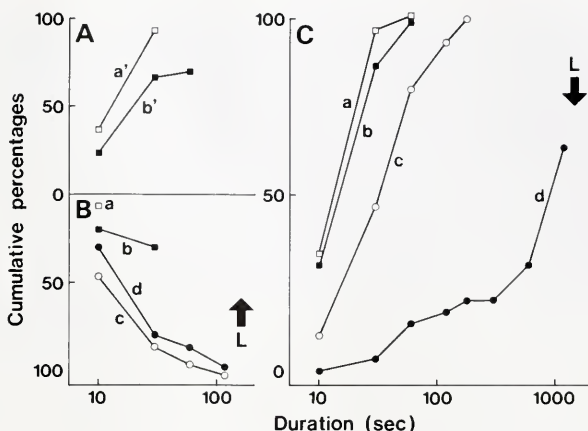


FIGURE 11. Effects of reduction in intensity of upward (A and B) and downward (C) directed light beams of 3000 lux. The reduced levels: 0 lux for curves *a* and *a'*, 3 lux for curves *b* and *b'*, 30 lux for curves *c* and 300 lux for curves *d*. Ordinates: Cumulative percentages of worms ($n = 30$) that responded with critical periods shorter than those shown on abscissae. A and C show the percentages of worms that moved upward. B shows percentages of downward moving worms, plotted in such a way that downward directed lines indicate higher percentages of downward movements.

rakami, 1959; Pearre, 1973; Nagasawa and Marumo, 1975; Kotori, 1976; Hirota, 1979; Goto, 1980). Light has been considered a major factor controlling these movements. However, most work has been done in the field and little attention has been paid to behavior or physiology of individual worms in relation to environmental conditions. In addition to confirming the findings of Esterly (1919) and Pearre (1973) that worms are basically negatively geotactic, coming to the water surface when placed in darkness (Fig. 4), and that a horizontal light beam of moderate intensities makes worms gather on an illuminated side (Fig. 1), we have presented several new facts regarding light-oriented movements of arrow worms, *Sagitta crassa* (summary diagram in Fig. 12).

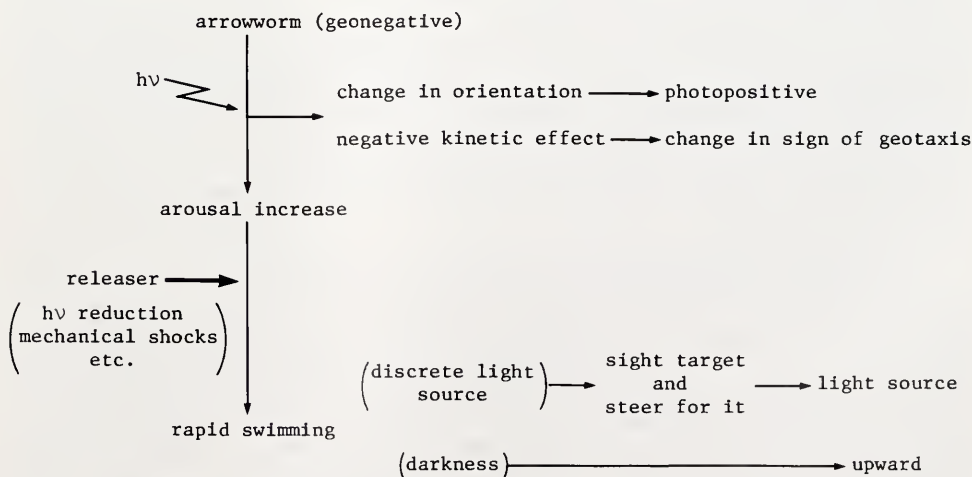


FIGURE 12. Summary diagram of the results.

When illuminated from the side, worms are rather slow to reach the illuminated end of a trough, even at the optimum light intensities to which all the worms respond positively (Fig. 1). Paths followed during this phototaxis show that the body axis of worms does not point directly toward the light source (Fig. 2). Instead, the body axis is significantly inclined toward light of moderate intensities, whereas in darkness and with brighter directed light, inclination toward one azimuth or another is more or less random (Fig. 3). Hence *Sagitta* shifts its position by repeated upward swimming movements with the body axis inclined toward the light source, interspersed with passive downward sinking.

The worms' more or less upright posture in darkness implies that they possess either a gravity sense or a gradient in specific gravity along the body axis, being heavier posteriorly. The latter possibility is not plausible, because when the worm is cut crosswise into three pieces, the head region sinks most rapidly. Also, anesthetized worms never sink with heads pointing upward. Since chaetognaths lack statocysts (Bullock, 1965), the gravity perception presumably is due to some other mechanism.

To induce light-oriented inclinations of the body axis, on the other hand, the effector system involved must be affected by gravity as well as information from light reception. Anterior, posterior, and tail fins, the bristles and cilia distributed over the body surface (Bone and Pulsford, 1978), and the ciliary loop on the dorsal side of the anterior region (Horridge and Boulton, 1967) are all possible candidates for the effector system. Other explanations, such as uneven contractions of the body wall by direct action of light, also are possible. It can be concluded that the light-oriented gathering is not a simple phototaxis or photokinesis, but is mediated by both gravity and light sensing mechanisms.

The quick target-aiming response induced by reduced light intensity (Figs. 6, 8, and 11), mechanical shocks (Fig. 9), etc., is an entirely new type of behavior in the laboratory. These two-step responses require a prior period of illumination during which the worms apparently do nothing, but become ready to respond to releasing stimuli (Fig. 12). On arrival of such a stimulus, the worms become kinetically active, and if those activated worms sight a target, they will steer toward it and start rapid swimming. In total darkness, they will swim upward due to their inherent negative geotaxis (see Figs. 4, 11, and 12).

The fact that worms presented with two targets do not swim along a resultant path of the two beams, but choose the brighter target (Fig. 10), may indicate that the behavior is a kind of telotaxis. Arrow worms possess a pair of pigmented ocelli. The pigment cell in each ocellus enables the receptive endings of sensory cells to differentiate incident light coming from various directions (Hesse, 1902; Burfield, 1927; Eakin and Westfall, 1964; Ducret, 1978; Goto, 1980). The existence of such a structure lends support to the notion of telotaxis, although, because of the delicate structure of the worm, direct proof by unilateral removal of the paired ocelli has not yet been obtained.

Chaetognaths are predators. They have been assumed to detect prey by sensing vibrations (Horridge and Boulton, 1967; Newbury, 1972). However, since the target-aiming swimming analyzed by us is quite accurate and rapid (14 cm per s), arrow worms may locate their prey visually and approach it telotactically when the prey (seen as a shadow) is swimming well outside the detectable range of vibration sensitivity, which is only 1–3 mm. Field observations of *Sagitta* feeding on larval herring (Lebour, 1923) suggest that our laboratory observations may have direct relevance to the predatory behavior in these animals.

However, *Sagitta*'s ability to catch prey at night and its simple lensless eyes

lead one to be suspicious of such a notion. It is perhaps more likely that the observed behavior is an escape reaction, although in such responses, which follow shading in many planktonic crustaceans, movement is mostly away from the shadow (e.g., Forward, 1974, 1976, 1977; Forward and Costlow, 1974). *Sagitta crassa* moves toward the shadow when only one light source is used. When more than one light source is used, the worms swim toward the brighter one. Such an ability would lead the worm in the sea to dodge away from approaching predators. Release of such reactions by mechanical shocks supports this interpretation. However, these speculations are based on experimental results obtained under laboratory conditions. The true biological significance of this unique swimming activity has yet to be directly demonstrated.

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